

SPATIAL OPTIMIZATION OF PRAIRIE DOG COLONIES FOR BLACK-FOOTED FERRET RECOVERY

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(Received October 1995; revision received July and August 1996; accepted January 1997)

A discrete-time reaction-diffusion model for black-footed ferret release, population growth, and dispersal is combined with ferret carrying capacity constraints based on prairie dog population management decisions to form a spatial optimization model. Spatial arrangement of active prairie dog colonies within a ferret reintroduction area is optimized over time for maximum expected adult ferret population. This modeling approach is applied in an exploratory case study to a black-footed ferret reintroduction program in Badlands National Park and Buffalo Gap National Grassland, South Dakota. The model is currently being used to evaluate prairie dog population management alternatives and captive-bred ferret release locations for the Buffalo Gap National Grassland. This approach is also being adapted for use on other grasslands and with other species in the northern Great Plains.

Early in 1987 the black-footed ferret (*Mustela nigripes*) became one of the world's most endangered mammals when the last known free-ranging member of the species was taken into captivity (Thorne and Belitsky 1989). The Wyoming Game and Fish Department was successful in breeding six of the surviving ferrets in captivity (Clark 1989). This set the stage for a national recovery program of releasing captive-bred ferrets back into the wild.

Historically, the black-footed ferret ranged sympatrically with prairie dogs (*Cynomys* sp.) across much of North America (Anderson et al. 1986). Available evidence strongly supports the conclusion by Henderson et al. (1969) that black-footed ferrets have narrow habitat requirements, living principally in prairie dog burrows and depending primarily on prairie dogs for prey (Linder et al. 1972). Demise of the species in the wild has been attributed to loss and fragmentation of habitat (prairie dog colonies) due to extensive prairie dog eradication programs and changes in land use, combined with susceptibility of prairie dogs to sylvatic plague and of ferrets to canine distemper (U. S. Fish and Wildlife Service et al. 1994). As Seal (1989) points out, it now appears difficult to find suitable ferret habitat complexes ("groups of prairie dog colonies in close proximity," Biggins et al. 1993) of 3,000 to

15,000 hectares, even though prairie dogs were once distributed over 40 million hectares of land.

The first release of captive-bred black-footed ferrets into the wild occurred in 1991 in Shirley Basin, Wyoming. Two additional reintroduction areas were added in 1994, including the site of this study centered in Badlands National Park, South Dakota. These ferret release sites were selected on the basis of habitat suitability and other biological and sociopolitical factors. Prairie dog population management within these sites will be a critical component in the success or failure of ferret reintroductions. Rodenticides are actively employed in the northern Great Plains, and have greatly reduced prairie dog populations (Roemer and Forrest 1996). Black-footed ferret recovery at the Badlands reintroduction site will likely be affected by the location and timing of rodenticide treatments in the area.

The spatial arrangement of prairie dog colonies in a colony complex has important effects on the number of black-footed ferrets that can be supported (Minta and Clark 1989). As prairie dog colonies become smaller or more widely separated, successful ferret dispersal between colonies is less likely and the total population that can be supported is reduced. Houston et al. (1986) and Miller et al. (1988) have employed spatial measures such as mean intercolony distance and colony size frequency distribution

Subject classifications: Natural resources: habitat allocation for endangered species recovery. Probability, diffusion: dynamic spatial population optimization. Programming, linear, applications: a black-footed ferret case study from South Dakota.

Area of review: OR PRACTICE.

in estimating ferret habitat suitability, but Biggins et al. (1993) note a number of troubling quantitative difficulties with such approaches. For example, it is often possible to identify a number of habitat patch arrangements that are equal in mean intercolony distance (as well as individual and total patch sizes) for which expected population responses would typically not be equal according to biodiffusion theory (Okubo 1980), island biogeography theory (MacArthur and Wilson 1967), or metapopulation models (e.g., Hanski 1994). Instead, estimates of pairwise dispersal between habitat patches are generally considered important. Consequently, in the Biggins et al. procedure, the effects of spatial colony arrangement within colony complexes are assessed qualitatively.

This paper presents the development of a more rigorous quantitative approach that is adapted from the theoretical spatial optimization work of Hof et al. (1994). In that approach, the ability of a modeled wildlife population to grow and expand was constrained by a combination of the inherent reproductive and dispersal characteristics of the species, and the size and arrangement of habitat, imposed as limiting factors. Hof et al. used binary habitat management variables to determine the resulting arrangement and carrying capacity conditions on a homogenous landscape over time. A continuous variable approach based on these ideas is presented here for black-footed ferret recovery. The model is used to explore habitat management and ferret release as a spatial efficiency problem on the federally managed lands of the Buffalo Gap National Grassland adjacent to the Badlands National Park ferret release area.

1. THE SPATIAL OPTIMIZATION MODEL

Within the reintroduction area, black-footed ferret habitat comprises a complex of active and potential prairie dog colonies (patches) forming distinct habitat "islands" on the landscape. The approach described here is related to earlier biodiffusion models (Skellam 1951, Kierstead and Slobodkin 1953), and island biogeography models (Allen 1987). Using a continuous reaction-diffusion equation for a single habitat patch with exponential population growth, Kierstead and Slobodkin established a critical patch size below which the population perishes. By discretizing the habitat into a number of individual patches, or islands—each too small to individually support a persistent population—Allen proved several important theorems, including the existence of a critical number of patches in a linear arrangement of such islands, below which the population again perishes. Our spatial optimization model retains these characteristics but uses discrete time periods and approximates habitat patch configurations with a grid of cells on the landscape. We then incorporate cellular habitat management decision variables so that all potential spatial configurations can be considered (within the resolution of our grid). With these decision variables to control the amount and location of ferret carrying capacity over time, our reaction-diffusion model can go beyond simply

evaluating persistence or extinction to estimating expected population size. Annual time periods also more closely model key ferret life history processes.

Ferret population growth and dispersal between cells from year to year is modeled here with an exponential population growth potential and a random dispersal pattern that relates probability of dispersal to distance. With discrete spatial cells and time periods, this reaction-diffusion process can be captured with linear constraints, as described below.

Rodenticide treatments, which have a negative effect on black-footed ferrets by reducing prairie dog numbers, are the principal habitat management action to be considered, as rodenticide applications are expected to continue on the National Grassland. Thus, a tradeoff exists between expected ferret population and the level (location, timing, and amount) of rodenticide use employed. Particular ferret habitat layouts are achieved over time by the prairie dog populations that result from the rodenticide treatment-nontreatment schedules applied to each cell across the landscape, on the premise that prairie dog populations will recover rapidly in areas left untreated. For any proposed habitat layout, the model is a useful method for estimating the expected ferret population over time. Beyond that, the model is also useful for finding efficient habitat layouts under various habitat (prairie dog population) policy constraints, so that the maximum number of ferrets can be supported given those constraints.

Decision variables (X_{ihk}) are defined for each possible schedule (indexed by k) of annual rodenticide treatment or nontreatment in each habitat condition class (indexed by h) for each cell (indexed by i). For example, one schedule could call for rodenticide treatments in the first year and every fourth year thereafter, while another schedule might call for treatments to begin in the second year instead. A third schedule could impose no treatments at all. Based on the number of hectares assigned to each habitat management decision variable (schedule X_{ihk}), adult black-footed ferret carrying capacity for a cell in any given year is then estimated from the prairie dog population expected under that management schedule. We will assume that no prairie dog populations would occur outside the selected habitat areas, although in practice, small numbers of prairie dogs can generally be expected.

Adult black-footed ferret populations expected in each cell in any year are limited by either the carrying capacity of that cell, or by the ability of ferrets from nearby cells to successfully reproduce and disperse there, or both. Additional decision variables (R_{it}) are used to determine the timing (year t) and location (cell i) for captive-bred ferret releases into the area. Release locations selected by the model are useful because locations for available ferret habitat are simultaneously scheduled. Due to their rapid dispersal, ferrets must be released in areas where ample prairie dog populations occur in the surrounding area as well as within the immediate vicinity in order to survive. The solution of the model indicates a complex of prairie

dog colony populations, over time, that supports a black-footed ferret population. Our spatial optimization model is:

$$\text{Maximize } F_T \quad (1)$$

subject to

$$F_t = \sum_i S_{it}, \quad t = 1, \dots, T, \quad (2)$$

$$S_{i0} = N_i \quad \forall i, \quad (3)$$

$$S_{it} \leq R_{it} + \sum_j g_{ji}(1 + r_j)S_{j(t-1)} \quad \forall i, \\ t = 1, \dots, T; \quad \sum_i g_{ji} \leq 1 \quad \forall j, \quad (4)$$

$$\sum_i R_{it} \leq b_t, \quad t = 1, \dots, T, \quad (5)$$

$$S_{it} \leq \sum_{h=1}^{m_i} \sum_{k=1}^{n_{ih}} c_{ihkt} X_{ihk} \quad \forall i, \quad t = 1, \dots, T, \quad (6)$$

$$\sum_{k=1}^{n_{ih}} X_{ihk} = A_{ih} \quad \forall i, h, \quad (7)$$

$$\sum_i \sum_{h=1}^{m_i} \sum_{k=1}^{n_{ih}} c_{ihkt} X_{ihk} \leq C_{pt} \quad \forall p, \quad t = 1, \dots, T, \quad (8)$$

$$X_{ihk}, S_{it}, R_{it} \geq 0 \quad \forall i, h, k, t,$$

with indices:

- t annual time periods $(0, \dots, T)$ that begin in late spring when the young emerge from the den;
- i, j habitat management cells in the study area;
- h initial habitat condition classes in each cell;
- k rodenticide treatment schedules;
- p policy constraints (if any) on selection of habitat management variables.

Decision variables:

- X_{ihk} amount of area (in hectares) in cell i and initial habitat condition class h allocated to the k th multiyear habitat management schedule;
- R_{it} number of captive-bred ferrets released in cell i during year t that are expected to survive adaptation to life in the wild.

Ferret population variables:

- S_{it} expected adult ferret population (including yearlings) in cell i at the beginning of year t , plus R_{it} ;
- F_t expected adult ferret population for the entire complex in year t .

Parameters:

- N_i actual or estimated initial number of adult ferrets in cell i
- g_{ji} proportion of surviving adult and juvenile ferrets from den areas in cell j in year $t - 1$ expected to disperse and become adult ferrets in cell i at the beginning of year t ;
- r_j an “ r -value” for ferrets in cell j reflecting the maximum expected annual net population growth rate (i.e., when habitat is not a limiting factor);

- b_t an upper bound on the total number of captive-bred ferrets released during year t expected to survive adaptation to life in the wild;

- c_{ihkt} expected adult black-footed ferret carrying capacity for cell i and condition class h in year t per hectare allocated to X_{ihk} ;

- m_i number of initial habitat condition classes in cell i ;

- n_{ih} number of habitat management schedules being considered for initial habitat condition class h in cell i ;

- A_{ih} total prairie dog colony area (in hectares) of initial habitat condition class h in cell i ;

- c_{ihkt} equals c_{ihkt} if X_{ihk} could contribute to policy constraint p in time period t , and zero otherwise;

- C_{pt} amount of total expected black-footed ferret carrying capacity allowed in time period t under policy p from the relevant subset of X_{ihk} habitat management variables.

Equations (1)–(5) define a discrete-time reaction-diffusion system (in this case, population growth and dispersal) for evaluating population persistence within a habitat complex. Equation (1) maximizes total expected adult black-footed ferret population at the end of year T , as summed by Equation (2). Equation (3) sets initial population conditions. Equation (4) limits the expected adult ferret population in any cell for any year to (at most) the number of captive-bred ferrets released into the cell plus the number of ferrets expected to disperse into the cell from all cells in the complex (including the same cell), after accounting for net reproduction during the previous year. Equation (5) limits the number of ferrets that can be released during any given year.

Reaction-diffusion models with areas of nonhabitat generally assume that organisms dispersing into unsuitable regions will perish. This mechanism provides a probabilistic basis for the expectation that, after accounting for births and deaths due to all causes in an abundant habitat setting through the r -value (net annual population growth rate r_j), additional mortality will occur in proportion to the usage of inhospitable surroundings. Equations (6) and (7) account for these habitat dynamics by imposing black-footed ferret carrying capacity constraints in each cell as a function of the selected habitat management (rodenticide treatment) schedules. The expected ferret population in any cell in a given year (S_{it}) is determined by either Equation (4) or (6), whichever is limiting. Individual or combined cellular carrying capacities may also be limited by prairie dog population management policies that restrict the availability of ferret habitat through Equation (8). We will employ Equation (8) to limit the total amount of ferret habitat in the National Grassland in order to examine spatially and temporally efficient tradeoffs between expected adult ferret populations and levels of prairie dog population control.

The linear dispersal model (Equation (4)) is based upon an assumption of purely random diffusion, which is a first-level approximation for highly developed species like the black-footed ferret. More realistic ferret dispersal patterns, if they were known, might exhibit biased diffusion, such as movement in response to overcrowding (Gurney and Nisbet 1975) or selective movement based on acquired knowledge of active prairie dog colony locations or surrounding terrain. In general, biased diffusion enhances the persistence of populations (Allen 1983). Thus, our model provides an estimated lower bound on the size of the expected population.

In some cases exponential population growth within patches may be unreasonably optimistic. For more conservative growth rates, sigmoidal population growth, by cell, could be approximated in a linear model by replacing Equation (4) with:

$$Q_{jt} \leq (1 + r_j)S_{j(t-1)} \quad \forall j, \quad t = 1, \dots, T,$$

$$Q_{jt} \leq S_{j(t-1)} + a_j \quad \forall j, \quad t = 1, \dots, T,$$

$$S_{it} \leq \sum_j g_{ji} Q_{jt} \quad \forall i, \quad t = 1, \dots, T,$$

where an accessory variable for cell population in each year (Q_{jt}) is limited to either exponential (r_j) or incremental (a_j) growth up to carrying capacity, depending on the magnitude of $S_{j(t-1)}$. Note that we have identified the r_j and a_j growth rates by cell. In some cases, expected net reproduction may be different from one cell to another even with abundant habitat. For example, one cell may lie closer to terrain frequented by predators than another cell. Exponential population growth (using an r -value) up to carrying capacity within cells, and random dispersal between cells, combine to provide a sigmoidal growth dynamic for total expected black-footed ferret population (F_t) when a persistent population is possible, even though cellular population growth is exponential.

Dispersal in Equation (4) assumes that ferrets within the complex originate from reintroduced animals. By limiting the total annual releases, as in Equation (5), the spatial optimization model is used to help identify preferred ferret release locations. In the event that release locations are predetermined, the annual release variables (R_{it}) could be individually limited instead of constraining the annual sums. We also assume that surviving released ferrets will disperse and reproduce similarly to indigenous ferrets. Additional mortality typical of released ferrets during the establishment period is accounted for by setting the upper bounds on releases (b_t) to the number of released ferrets that are expected to survive and reproduce. If released ferrets were known to initially disperse or reproduce at rates different from wild-born ferrets, Equation (4) could be replaced with:

$$S_{it} \leq \sum_j [g_{ji}(1 + r_j)S_{j(t-1)} + g_{ji}^R(1 + r_j^R)R_{j(t-1)}] \\ \forall i, \quad t = 1, \dots, T, \quad \sum_i R_{i0} = 0.$$

This would defer accounting for releases in the S_{it} and F_t variables for one year.

The linear programming approach used here leaves unresolved the specific locations of habitat resulting from different treatment schedules within a cell. The choice of cell size controls the spatial resolution of the model. If large cells are used, rodenticide treatment locations would be less well-specified, which could reduce the accuracy of the g_{ji} dispersal coefficient estimates. The size of these errors can be controlled by using smaller cells, in a manner typical of numerical approximations. As smaller cells are employed, the habitat location and associated dispersal estimation errors approach zero, but model size increases. In practice, some compromise is required to address large-scale problems. Dispersal estimation errors will generally be reasonably small if we define habitat management cell sizes that are small relative to ferret dispersal ranges.

In cases like black-footed ferret reintroductions, where initial conditions differ greatly from potential persistent population levels, habitat conversion strategies based on prairie dog population management decisions in the first several years can be as important as long-term management strategies. The relative weight placed on short-term versus long-term management depends primarily on the choice of objective function (e.g., Bevers et al. 1995). While the objective function expressed in Equation (1) is suitable for estimating persistent (long-term) expected ferret population levels, another objective function was also used in the case study to place more emphasis on early ferret establishment. We replaced Equation (1) with:

$$\text{Maximize:} \quad \sum_t F_t, \quad (9)$$

for all analyses except those focused on long-term persistence.

2. FERRET REINTRODUCTION IN SOUTH DAKOTA

Between September 19 and November 14, 1994, 36 captive-bred black-footed ferrets were released near the center of the Sage Creek Wilderness in Badlands National Park (McDonald 1995). This was the first of five annual releases planned for the purpose of reestablishing ferrets in the Park and the surrounding Buffalo Gap National Grassland (Plumb et al. 1994).

We applied the spatial optimization model to a region approximately 157,500 hectares (ha) in size surrounding the South Dakota reintroduction area, assuming that prairie dog population controls will preclude ferret recovery outside this study area. Federally managed lands with active (supporting substantial live prairie dog population densities) or readily recoverable inactive black-tailed prairie dog (*C. ludovicianus*) colonies suitable for ferret habitat over the next 10–15 years are fragmented, occupying less than one-tenth of the study area. Badlands National Park contains an estimated 2,403 ha of active prairie dog colonies, primarily in the rugged Sage Creek Wilderness. This acreage is not expected to change significantly over

the next 10-15 years. Under current management plans, Buffalo Gap National Grassland supports an estimated 2112 ha of predominantly active prairie dog colonies reserved from rodenticide use adjacent to Badlands National Park. We refer to these as "current" colonies. The Grassland contains an additional estimated 9850 ha of predominantly inactive prairie dog colonies in the study area which have been treated with rodenticide in past years. We refer to these as "potential" colonies.

Spatial Definition

We selected U. S. Public Land Survey sections as cells for the model and assumed for dispersal probability calculations that each of the 608 survey sections (indexed by i) in the study area was a square enclosing 259 ha of land. The number of hectares of existing prairie dog colonies within each section were estimated from color infrared aerial photography taken in August of 1993 using methods described by Schenbeck and Myhre (1986) and Uresk and Schenbeck (1987). Active prairie dog colony areas within these intact burrow systems were inventoried from field survey records. Inactive areas were identified as readily recoverable for the next 10-15 years, along with areas having intact burrow systems identifiable in similar aerial photographs taken in 1983. The 1983 prairie dog colony distribution was used to estimate potential colony distribution because this was the period when recorded prairie dog populations were greatest. Other suitable prairie dog habitat areas lacking burrow systems since 1983 were not inventoried for this model, under the assumption that population establishment in those areas is beyond the 10-15 year time frame of interest. Land areas within each survey section were classified as either National Park Service administered lands ($h = 1$), USDA Forest Service administered lands presently subject to prairie dog population control (potential, $h = 2$), or USDA Forest Service administered lands presently reserved from prairie dog population control (current, $h = 3$). Privately owned lands were not included in the model.

Ferret Dispersal

Although relatively few observations of ferret movements are available, distances of 2-3 km were typical for both nightly movements and annual intercolony movements (primarily by juveniles in late summer or early autumn) of wild-born ferrets at Meeteetse, Wyoming (Forrest et al. 1985, Biggins et al. 1986, Richardson et al. 1987). The longest nightly move reported from that complex is about 7 km. Oakleaf et al. (1992, 1993) report substantially longer dispersal distances (up to 17.5 km) over the first 30 days following captive-bred ferret releases at the Shirley Basin prairie dog colony complex in Wyoming. The statistics reported by Oakleaf et al. roughly suggest an exponential distribution of dispersal distances, while dispersal was apparently equally likely in all directions (although few observations are available). Eight of the ferrets released in Badlands National Park in 1994 were observed to disperse

with a mean distance of 3.7 km and a maximum distance of 11.8 km (standard deviation = 4.2 km) over about a 30-day period. It is not known to what degree differences between these observations result from differences between captive-bred and wild-born ferrets, differences between prairie dog colony complexes, or from other causes.

For this study, we assumed that all ferrets will disperse annually according to an exponential distance distribution with a mean of 3.7 km in uniformly random directions over a radius of about 14 km. Dispersal coefficients (g_{ji}) were then estimated by numerical approximation of the integral of this bivariate dispersal distribution over distances and angles defined by the boundaries of each destination (i) section relative to the center of each source (j) section. The effects of rugged topography in the Badlands could be taken into account in the pairwise estimation of dispersal coefficients, but these effects are unknown.

Net Population Growth Rate

Wild ferrets have not been studied under conditions of unlimited habitat. Consequently, values for r_j were estimated by simulating unlimited population growth using mean birth and death rates and initial conditions similar to those assumed by Harris et al. (1989) in their research on black-footed ferret extinction probabilities. Beginning from expected values of 1 male (yearling or older), 1 yearling female, and 1.2 adult females (two years old or older), the simulated population was iteratively grown year by year. Yearling females were expected to produce 0.85 litters each, while adult females were expected to produce 0.95 litters each. Each litter was expected to produce 1.7 juvenile males and 1.7 juvenile females. Mortality then removed half of the juvenile males, 40 percent of the juvenile females, 20 percent of the adult males, and 10 percent of the adult and yearling females. After 12 simulation years the population ratios and growth rates stabilized with an r -value (annual net population growth rate) of 0.8175.

Ferret Releases

Based on past experiences (Oakleaf et al. 1992, 1993), approximately 80 percent of released captive-bred black-footed ferrets are expected to die during their first 30 days in the wild. Half of the remaining ferrets are expected to perish during their first winter. Of the 36 ferrets released in Badlands National Park in 1994, only eight were known to survive the first 30 days. Taking into account likely winter mortality, we assigned an expected population value of 0.5 adult ferrets at each of the eight surviving ferret locations as initial conditions (N_i) in the model (with zeroes assigned elsewhere).

We expected 40 more ferrets to be released in the fall of each of the following four years. Assuming that four ferrets from each release would survive to reproduce, we set $b_1 - b_4$ equal to 4.0 (with zeroes assigned for all other years).

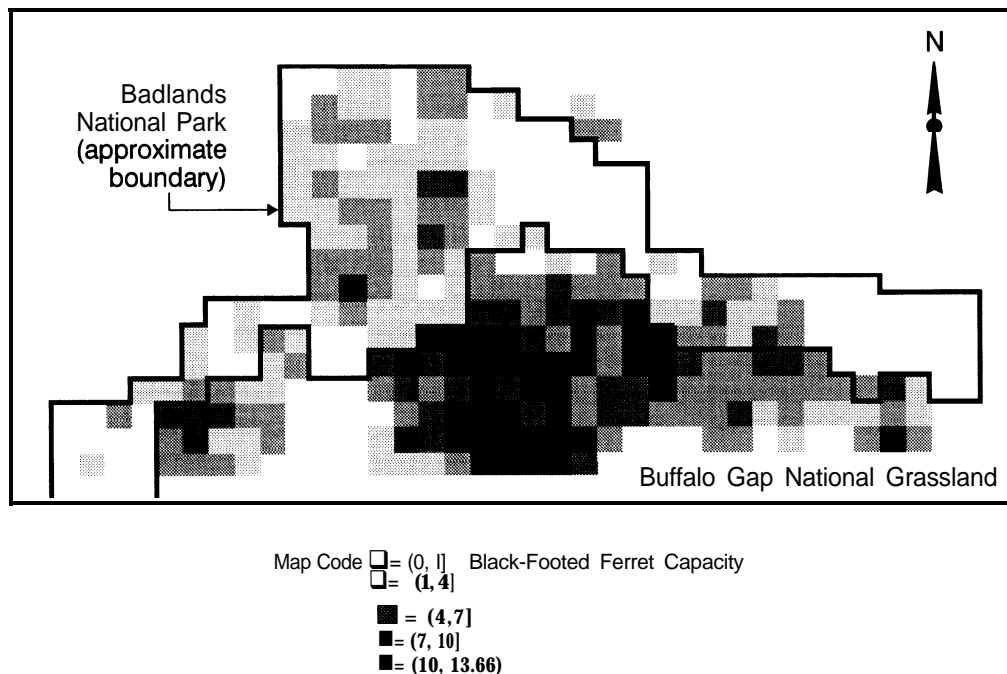


Figure 1. Available short-term (10-15 year) adult black-footed ferret carrying capacities on federally managed lands within the study area.

Ferret Carrying Capacity

Although prairie dog densities within colonies typically decline over extended periods of time (Cincotta 1985, Hoogland et al. 1988), existing colonies in the Badlands area for the next 10-15 years are expected to remain well above the lower limit of "good" ferret habitat (3.63 prairie dogs/ha) estimated by Biggins et al. (1993). Consequently, we based our estimate of maximum ferret carrying capacity on the observations reported by Hillman et al., (1979) of ferret populations in Mellette County, South Dakota. In the model, adult ferret carrying capacities (C_{ihkt}) on existing or fully recovered prairie dog colonies were set at 0.05273 ferrets/ha. Figure 1 shows the spatial arrangement of current plus potential ferret habitat by survey section in the study area at maximum model carrying capacity (determined by summing $0.05273 A_{ih}$ across h for each section i). Carrying capacity for the entire area was about 757 adult ferrets. Most of the ferret carrying capacity shown on the National Grassland (outside of the Park boundary) is potential rather than current habitat, comprising predominantly inactive prairie dog colony burrow systems. This does not necessarily inhibit ferret establishment on the Grassland in our model, however, because prairie dog populations can generally recover more quickly than ferret populations can be established.

Potential prairie dog colonies are not presently able to support ferrets at maximum carrying capacity due to past treatments with rodenticide. Based on studies by Knowles (1985), Cincotta et al. (1987), and Apa et al. (1990), we estimated that complete prairie dog population recovery in recently treated colonies would require an average of four

breeding seasons. We set adult ferret carrying capacity (c_{ihkt}) accordingly at one-eighth of full capacity (0.00659 ferrets/ha) for the first year following use of rodenticide, at one-fourth of full capacity (0.01318 ferrets/ha) for the second year, at one-half of full capacity (0.02636 ferrets/ha) for the third year, and at full capacity thereafter (given no additional rodenticide treatments). This rate of recovery could require special management actions, such as intensive livestock grazing, to aid the spread of prairie dogs (Uresk et al. 1981, Cincotta et al. 1988). We also assumed that all potential habitat areas in the model could begin recovery in any chosen year.

3. MODEL RESULTS

The model was solved on a personal computer using Ketron's commercial linear programming package "C-Whiz," with Equation (9) as the objective function. Equation (8) was used in six separate optimizations with different right-hand side (C_p) levels to restrict the amount of ferret carrying capacity added from potential prairie dog colonies on the Grassland ($h = 2$) to form a tradeoff analysis. Thus, for each of the six alternatives, a single policy constraint ($p = 1$) was used with identical right-hand-side amounts for each year t . The X_{i2k} decision variables were given nonzero C_{ihkt} coefficients for years in which no rodenticide treatments were scheduled. All other decision variables were given C_{ihkt} coefficients of zero. A 25-year planning horizon ($T = 25$) was used to allow enough time for expected ferret population levels to stabilize, but care must be taken not to overinterpret results beyond 10-15 years.

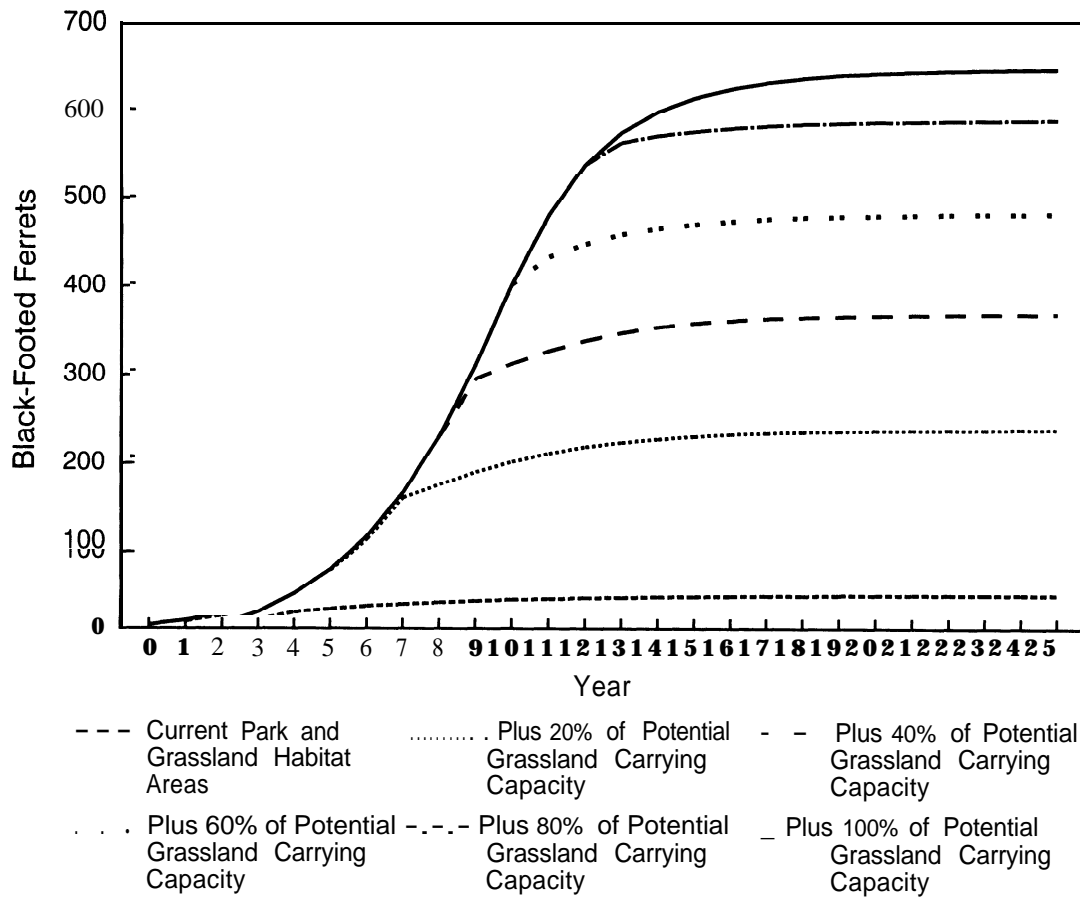


Figure 2. Expected adult black-footed ferret populations under the present management strategy and five alternative strategies.

Beyond 15 years, additional potential prairie dog habitat might need to be considered, as well as the possibility of declines in prairie dog population densities for older colonies.

Figure 2 shows the total expected adult ferret population (F_t) resulting from allowing no additional carrying capacity ($C_{pt} = 0$), and from five 20-percent increments of habitat (capacity for 103.88 additional adult ferrets per increment) from the potential Grassland prairie dog colonies. The lowest expected population curve in Figure 2 results from using rodenticides to prevent any increase in prairie dog populations from current levels ($C_{pt} = 0$). The highest expected population curve results from discontinuing rodenticide use in the area altogether ($C_{pt} = 519.4$). Due to ferret dispersal, increments of additional ferret carrying capacity do not result in proportional increases in expected ferret population.

In all cases in Figure 2, sigmoidal expected population growth curves resulted. As we would expect, the graph shows diminishing marginal returns as more carrying capacity is added because the most spatially efficient habitat areas are included first. Also, each curve levels off substantially below total allocated carrying capacity. For example, when all Grassland habitat areas are allocated to prairie dog colonies, the expected population of ferrets rises to

only about 85 percent of the summed capacity of more than 757 adult ferrets. This suggests that simply totalling available carrying capacity will tend to overestimate the population size that can be supported because spatial arrangements are not taken into account.

Preferred habitat areas change over time, as shown in Figure 3 by maps of the habitat allocated in different years (expressed as adult ferret capacity, calculated by summing $c_{ihkt}X_{ihk}$ across h and k for each i and t) under the alternative which adds 20 percent of the potential Grassland carrying capacity for ferrets. The 20-percent limit for this alternative is binding from year 7 on. Prior to that year, the expected ferret population is still small enough that the constraint is not limiting. Figure 3a shows the habitat allocations for year 7. Survey sections outside of the Park and current Grassland colony areas (outlined in the figure) are potential habitat, where management choices (schedules of rodenticide treatment) were allowed. In Figure 3a, a small amount of habitat is allocated to all but one survey section with potential habitat because the fledgling expected ferret population is rapidly expanding throughout the area (compare with Figure 1). The expected population in year 7 (S_{i7} for each section i) is shown in Figure 4b, along with the corresponding selected ferret releases (the sum of R_{it} across t for each section i) shown in Figure 4a.

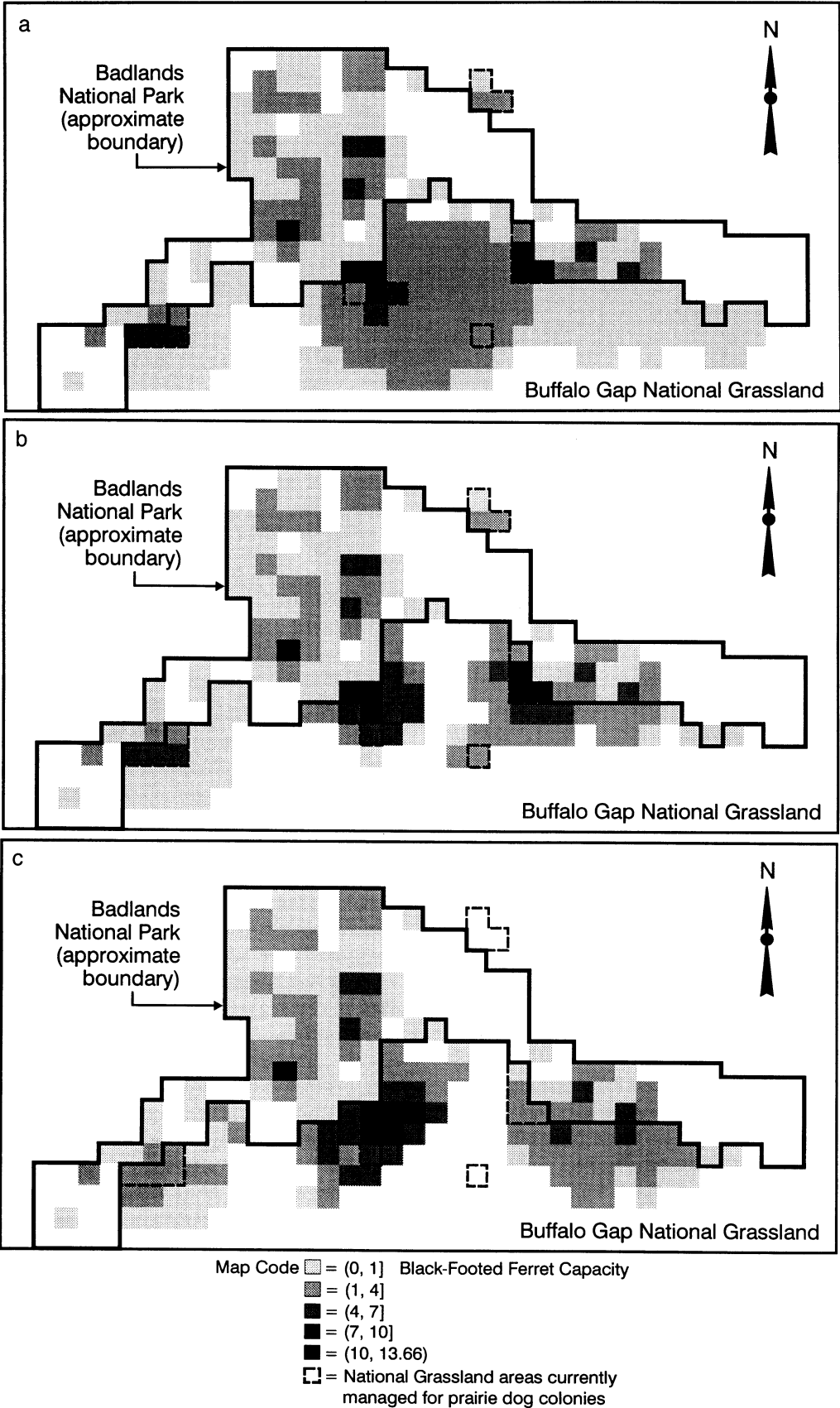


Figure 3. Habitat allocations expressed as adult black-footed ferret carrying capacities under the +20% alternative (a) in year 7, (b) in year 15, and (c) near equilibrium.

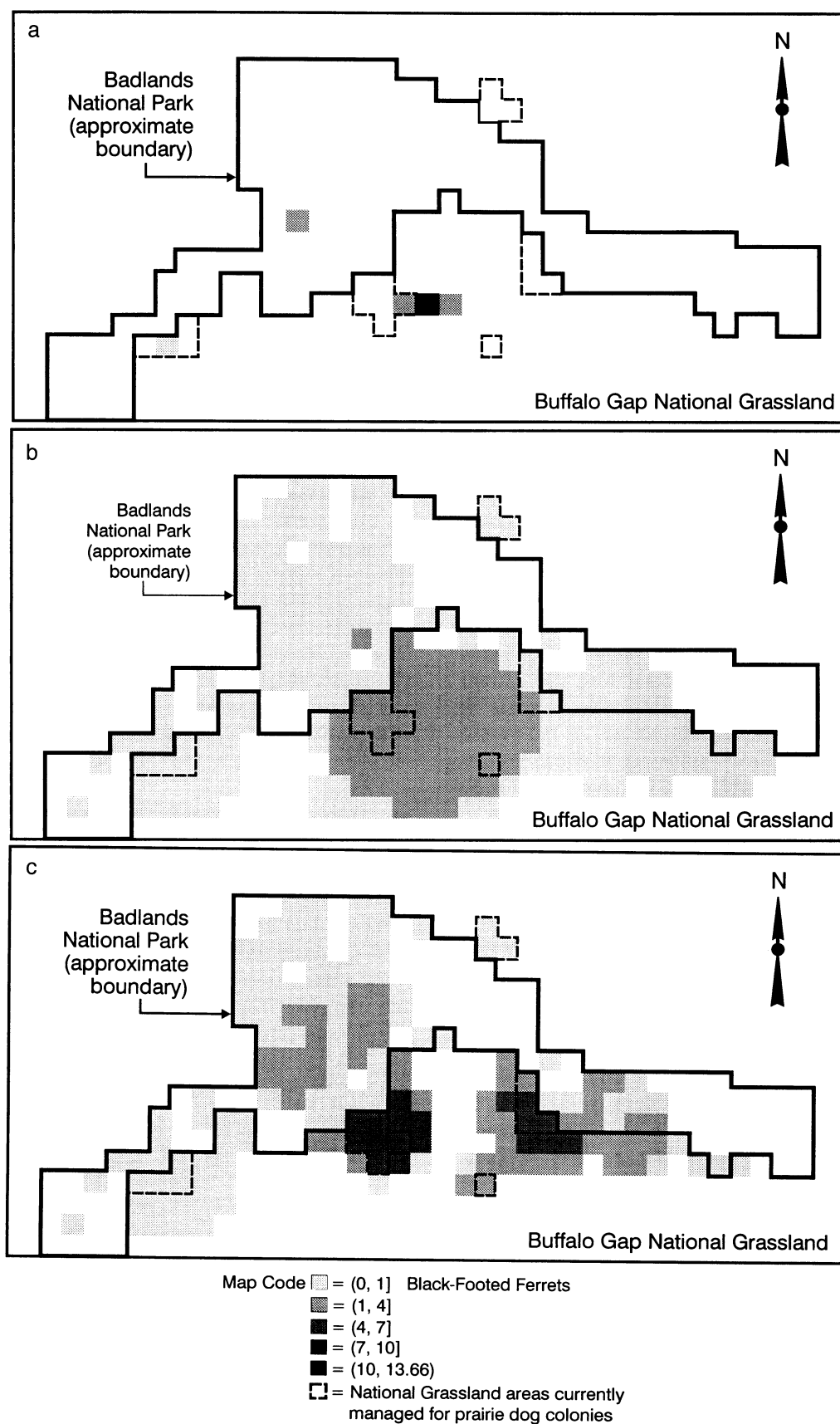


Figure 4. The expected number of adult black-footed ferrets by location under the +20% alternative (a) released at selected sites, (b) in year 7, and (c) in year 15.

By year 15, the expected ferret population under this alternative has largely leveled off at more than 230 adult ferrets, and the preferred habitat allocations have shifted to more concentrated areas around the Park and current Grassland colonies (Figure 3b). Many survey sections 'which had some habitat allocated in year 7 no longer have any habitat allocated by year 15. The corresponding expected ferret population (S_{i15} for each section i) is shown in Figure 4c.

Based on these results, we examined the habitat allocations for this alternative near equilibrium conditions by bounding all ferret release variables to zero (R_{it} in Equation (5)), unbounding all initial population variables (S_{i0} in Equation (3)), and using Equation (1) as the objective function. With initial populations no longer restricting the solution, a static equilibrium can be approximated without the need for building a different model. We also allowed the model to schedule treatments for Grassland colonies currently reserved from rodenticide use ($h = 3$) in addition to potential colony ($h = 2$) treatments for meeting the policy constraint to allow greater spatial freedom for habitat selection. The resulting allocations (Figure 3c) support an expected population that levels off at a little more than 300 adult ferrets. This is an increase of about 60 adult ferrets (in year 25) over the alternative that optimally combined 20 percent of the potential Grassland with the current prairie dog colonies (see Figure 2). The increase is achieved by exchanging some (but not all) of the prairie dog colonies from the current colony areas for new colonies in the nearby Grassland areas (compare Figures 3b and 3c). While this near-equilibrium analysis appears to extrapolate beyond the supporting data due to the length of time involved, this may not be the case. If black-footed ferret dispersal is actually a biased diffusion process, the population might be able to take advantage of highly concentrated habitat more quickly than our results would indicate.

The pattern of Grassland allocations in Figure 3c results from the interaction of two important effects. Many of the sections with the highest potential ferret capacity are left unallocated by the model in order to round out the long, narrow habitat arrangements in portions of the Park. In the model, population losses from fully occupied habitat occur from dispersal across the habitat perimeter into unsuitable areas, and from dispersal into areas already at carrying capacity. For a given amount of habitat, carrying capacity remains constant while dispersal losses into non-habitat areas can be lowered by changing the shape of the area to reduce dispersal across the perimeter. Allocating circular patterns, which have the smallest perimeter-to-area ratio, would minimize losses and maximize retained population given uniformly random dispersal direction. This tendency appears to be compromised somewhat in favor of placing habitat close to as many sections of the Park as possible.

The results described thus far were obtained using enough different management variables (coupled with

Table I
The Expected Number of Black-footed Ferrets in Each Year for the +20% Alternative under Three Different Scheduling Formulations

Year	Allocation in Year 1	One-Time Allocation Change in Any Year	Full Scheduling Model
1	9	9	9
2	17	17	18
3	31	31	32
4	51	51	53
5	76	76	79
6	106	107	114
7	139	139	161
8	163	169	177
9	182	183	190
10	196	195	202
11	205	204	212
12	212	210	219
13	217	216	225
14	220	219	229
15	222	222	232
16	224	224	234
17	225	225	236
18	225	226	237
19	226	227	238
20	226	227	238
21	227	228	239
22	227	228	239
23	227	228	239
24	227	228	240
25	227	228	240

constraints on carrying capacity rather than on land allocations) to provide a great deal of flexibility in ferret capacity placement and timing through the selection of spatially defined rodenticide treatment schedules. However, such flexibility may be impractical. Public land use planning for a 10-15 year period is often viewed as a process for scheduling a one-time change (if any) in management. To test the effects of that approach, we constructed a model in which the potential Grassland management variables (X_{i2k}) were redefined to form a more restrictive set of options. Although the model could choose when to stop rodenticide treatments in a particular area (if at all), no further treatments could be scheduled afterward. In some planning cases, scheduling is not even considered, and all management changes take immediate effect. To test those effects, we constructed another model in which the management variables for each potential section (again, X_{i2k}) simply represented either repeated rodenticide treatments or none at all. Table I shows the yearly expected adult ferret populations (F_t) using these different approaches for the alternative that allocates 20 percent of the potential Grassland carrying capacity (in addition to the Park and current Grassland colonies). Considering the small differences in Table I, the use of simpler models (with greater ease of presentation and implementation) may not impact results significantly.

The reductions in matrix size and complexity with the simpler models were substantial. The full scheduling formulation included 20,946 rows and 65,598 columns, while the simpler "one-time change in management" scheduling model reduced the problem size to 17,795 rows and 21,972 columns. The nonscheduling model further reduced the number of columns to 18,156.

4. CONCLUSION

Our model is the first application of this type of dynamic spatial optimization to a real-world problem of habitat evaluation and management design. With very limited knowledge of ferret reproduction and dispersal in the wild, the model results must be regarded as an initial estimate of a lower bound on expected population levels for a given habitat arrangement. The method appears to be promising in aiding with efficient design of alternative habitat management and reintroduction strategies. The explicit accounting of spatial patch relationships, as opposed to relying on measures like mean intercolony distance, is the strong point of the model. Viewing the model's expected population estimates as lower bounds provides a useful contrast to results from habitat complex circumscription methods (e.g., Biggins et al. 1993), which could probably be viewed as estimates of expected population upper bounds, at least prior to any qualitative adjustments. For species with highly random dispersal behavior, the spatial optimization estimate of expected population should be especially useful.

An evaluation of the Buffalo Gap National Grassland prairie dog management and black-footed ferret recovery program began in 1996 as part of a land management planning process for national grasslands across the northern Great Plains. This spatial optimization model and other published ferret models will be the principal tools for scientific review in that evaluation. Our model has already been used to demonstrate the importance of monitoring ferret dispersal, as well as survival and reproduction. Biologists are currently gathering data for refining and validating our model for future use, and are adapting the model to other reintroduction areas. These reaction-diffusion methods have also been adopted for analyzing habitat alternatives for other threatened and endangered species in the northern Great Plains.

We must stress that the spatial optimization model is deterministic, and produces estimates of expected population. Stochastic variation, which can be a particularly important consideration at low population levels, is not taken into account. Stochastic variation in net population growth has been accounted for in a model developed by Harris et al. (1989) for estimating black-footed ferret population viabilities as functions of initial population size. Replacing initial population size in their viability model with expected population size from our spatial optimization model would provide a lower bound estimate of expected viability which takes into account stochastic variation in

net population growth. For some purposes, this might provide an additional benefit by reducing results to a probability-based index. However, stochastic variation of other important model parameters remains unaddressed.

Clearly, there is much we do not yet know about black-footed ferret populations in the wild. More information on ferret dispersal could be particularly useful. Consequently, the actual response of the new South Dakota population will likely be different from model predictions, at least in terms of ferret densities. As more is learned through ferret monitoring over the next several years, we anticipate that the model could be used as part of an adaptive management process (Walters 1986). The spatial optimization model offers a great deal of flexibility for combining site-specific habitat and population information (as it becomes available) with management options and constraints. Further research is needed to understand the complexities of ferret and other wildlife population dynamics, and to account for those complexities in optimization modeling.

ACKNOWLEDGMENTS

The authors wish to thank Kieth Severson, Helen Fitting, and Peter McDonald for providing information and data, and Jill Heiner for computer programming used in this study. The manuscript was substantially improved through the efforts of the editors and two anonymous referees.

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